The angular gyrus is engaged by autobiographical recall not object-semantics, or event-semantics: Evidence from contrastive propositional speech production

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Abstract

A long history of neuropsychology and neuroimaging has implicated the angular gyrus (AG) with a myriad of cognitive functions. We investigated the functional engagement of AG by three forms of memory: 1) episodic/autobiographical memory 2) object semantic-memory, and 3) event-semantic processing using the previously under-examined naturalistic task of propositional speech production. We conducted an ALE meta-analysis of imaging studies of propositional speech, followed by an fMRI study in which we conducted direct cross-domain comparisons. The results from the meta-analysis suggest that the AG is only engaged as part of the propositional speech network when the task carries an autobiographical component. This conclusion was strongly supported by the results from the fMRI study. The key fMRI findings were: 1) AG was positively engaged during autobiographical memory retrieval. 2) The AG was strongly deactivated for definitions of object semantics and non-propositional speech. 3) The level of AG activation increased with the degree to which the event descriptions relied on input from the episodic memory system. 4) Critically, the AG showed a very different pattern to that of known semantic representation regions (the anterior temporal lobe; ATL) - whilst AG activation increased with the autobiographical nature of the task, the ATL was equally responsive to all conditions. These results provide clear evidence that the AG is not acting as a semantic hub. In contrast, the AG activation profile directly mirrored that found in the wider autobiographical retrieval network. We propose that information stored elsewhere in the episodic system is temporally buffered online in the AG during autobiographical retrieval/memory construction.

Keywords: Angular gyrus, Episodic, Autobiographical, Semantic, Event, Propositional speech production

Introduction

A long history of neuropsychology and neuroimaging has implicated the lateral parietal cortex (LPC) with a myriad of cognitive functions. Whilst highly sophisticated models exist for each domain in isolation, the majority of theories fail to account for the variety and potential functional overlap of LPC activities. There are two alternative ways that the LPC might be organised: 1) A form of 'neuromarquetry' in which LPC contains numerous discrete sub-regions each recruited by different tasks and serve distinct underlying cognitive functions; or 2) shared computations - multiple cognitive activities rely, in common, upon a small number of common underlying computations that arise from the LPC and its patterns of connectivity to the wider neural network. Resolving this puzzle will necessitate direct cross-domain comparisons. Two domains that have heavily implicated the LPC, specifically angular gyrus (AG), are episodic memory and semantic memory retrieval. For instance, one model proposes that the AG forms an episodic buffer for retrieved episodic information (1, 2). An alternative to the episodic hypothesis is that AG is a semantic-hub that stores multi-modal semantic information (3-5). A related though more specific alternative to the semantic-hub hypothesis is that the AG stores "semantic event" information per se, whereas "object" information is stored elsewhere in the semantic system, such as the anterior temporal lobe (ATL) (6). Alternatively, others have proposed domain general models, for instance the theory that AG is implicated by any "internally-generated" cognition (including semantic memory or episodic memory retrieval, as well as other processes) (7, 8), or that it forms a multi-modal sequential buffer (9-11). In addition to the confusing number of potential roles of the AG, the majority of the studies have investigated "input" modalities (e.g. making a decision on written/auditory words or pictures), whereas relatively few have looked at "output" tasks, such as speech production.

Direct within-study comparisons.

A test of these alternative hypotheses of AG function requires direct cross-domain within-study comparisons. A recent functional magnetic resonance imaging (fMRI) study manipulated internally vs. externally directed attention, and episodic retrieval vs. semantic retrieval (12) There were four conditions, two involving internally directed attention (semantic retrieval or episodic retrieval) and two involving externally directed visual attention (real-world object decision, or scrambled pattern decision). The AG (subregion PGp), a region that overlaps with the default mode network (DMN), was found to show strong positive activation during episodic retrieval, with the level of activation correlating with item-specific memory vividness ratings. In contrast, the AG showed deactivation relative to rest and relative to the control task, with the level of deactivation correlating with task difficulty (stronger deactivation for the harder items). Functional and structural connectivity analyses found that the same AG region of interest (ROI) showed connectivity with the wider episodic retrieval network, including the medial temporal lobes, as well as medial prefrontal,

precuneus, and posterior cingulate cortex (13-15), consistent with existing evidence (12, 16-19). Combined, these data appear to support functional involvement of the AG in episodic retrieval rather than involvement in semantic retrieval or the processing all forms of internally-generated thought. Nevertheless it does not preclude the possibility that the central function of AG is "semantic event" knowledge since episodic retrieval might necessitate the activation of event semantics. The results are also consistent with the Parietal Unified Connectivity-biased Computation (PUCC) model (9-11), whereby the emergent expressed function will depend on what sources of information and influences arrive at each subregion, in this case the AG connect with the episodic retrieval network and hence is more engaged by tasks that involve episodic retrieval. Note that PUCC and the "episodic buffer" model are not mutually exclusive, PUCC simply offers a mechanistic explanation as to how an episodic buffer might operate.

Propositional speech production as a useful paradigm to investigate AG function

The current study used a propositional speech production paradigm to determine the underlying function of AG whilst also addressing a number of existing limitations in the literature. Speech production was used for four primary reasons: 1) relatively little is known about the involvement of IPL, including AG, in expressive tasks since existing theories are based almost exclusively on "input" tasks (e.g., word recognition); 2) Propositional speech is inherently "internally-generated" and thus makes the ideal testing environment to determine to what extent the AG is recruited for a variety of internally-generated domains generated (semantic, episodic etc.); 3) Speech production can be a powerful and flexible paradigm to investigate cognitive function as one can carefully manipulate the speech topic (e.g., semantic definition vs. autobiographical description) and thereby influence the degree to which different subsystems are drawn upon to produce speech content; 4) Finally, narrative speech production is a time-extended behaviour that therefore provide insights into the internal operation of a "temporal buffer" model. The current literature on speech production and the AG is sparse, and provides mixed support for its engagement. A few studies have found that AG is actively engaged when participants answer questions, such as "tell me about the last family gathering you attended" (20, 21). However, others have found greater AG activation when performing non-verbal tongue movements compared to meaningful speech production (providing definitions of a noun) (22). The reason for this discrepancy in results is unclear. For instance, of relevance here, these studies cited varied in terms of speech topic; LPC activation was observed for the autobiographical description task but not a noun-definition task. However, there are numerous other variations across studies (e.g., speech duration, PET vs. fMRI, covert vs. overt speech). Therefore, the existing research is hard to interpret based on the wide variety of tasks utilised.

The current study sought to examine whether the AG is engaged during speech production, and if so, what cognitive variables modulate AG engagement. We first conducted a meta-analysis of the existing propositional speech production neuroimaging studies in order to determine the reliability of AG effects, and the extent to which they are influenced by task-related variables. Whilst meta-analyses are powerful techniques that highlight generalizable results across studies, they can blur data thereby losing the anatomical precision that can be derived from direct within-study manipulations. Therefore, we conducted a within-subject cross-domain fMRI study in which we directly manipulated narrative speech content. Specifically, the participants provided verbal responses to a number of questions during the fMRI task. There were four varieties of question: 1) autobiographical condition: the participants answered questions asking about specific past events (e.g., describe the last time you drank a cup of tea); 2) semantic-event condition: the participants described how a particular event would typically unfold (e.g., describe how you would typically make a cup of tea); 3) semantic-object condition: the participants provided semantic-definitions of objects (e.g., what is tea?); and, 4) control condition: a non-semantic speech control task (recite the months of the year).

Methods

Meta-analysis

Study selection: The meta-analysis comprised of 26 PET and fMRI studies that included a sentence- or narrative-level propositional speech production paradigm compared to a control condition or resting baseline. Only those that reported peak activation in standard space (Talaraich or MNI) based on whole-brain statistical comparisons were included. The studies were identified by searching through studies highlighted by keyword searches using Google Scholar (keywords included: "speech production", "speech generation", "propositional speech", "sentence", "narrative", "verbal description", "fMRI", "PET"), as well as from related existing meta-analyses (23-25), and citations from within those relevant papers. Examples of typical contrasts were: define a noun > counting, sentence generation (based on key words) > sentence reading, sentence generation (based on picture) > rest. Amongst the selected papers, six studies included autobiographical manipulations (e.g., the participants were asked questions such as "what did you do last weekend?" compared to counting).

ALE analyses: The ALE analyses were carried out using GingerAle 3.0.2 (26, 27). All activation peaks were converted to MNI standard space using the built-in Talairach to MNI (SPM) GingerALE toolbox. Analyses were performed with voxel-level thresholding at a p-value of 0.001 and cluster-level FWE-correction with a p-value of 0.05 over 10,000 permutations. In order to identify the network engaged by propositional speech production, the initial analysis was performed including all 26 studies. Then, secondary analyses were conducted in order to examine specific task-related

effects. In particular, we sought to determine the extent to which the activation likelihood maps were influenced by the inclusion of studies using autobiographical manipulations. This was done by removing the six autobiographical studies and re-running the ALE analysis using the remaining 20 studies. Since changes in the activation likelihood maps from the first analysis (26 studies) with the second analysis (20 studies) could be due to reduction in power rather than an influence of autobiographical task per se, we performed additional analyses in which six studies from the original pool were excluded at random, the results of which could be compared to the new 20 study-pool. The random study-exclusion analysis was performed 10 times in order to observe which clusters from the activation likelihood maps were stable, thereby implying they form a core feature of the propositional speech network, and which clusters varied, thereby implying task-modulation.

fMRI study

Participants

Twenty-eight participants took part in the fMRI study (average age = 27.91 years, SD = 6.19; N female = 20). All participants were native English speakers with no history of neurological or psychiatric disorders and normal or corrected-to-normal vision. The fMRI experiment was approved by the local ethics committee. Written informed consent was obtained from all participants.

Task design and procedures

There were four experimental conditions: autobiographical description, semantic-event description, semantic object description, and control condition. Each trial involved two phases; memory retrieval phase and response phase. In the memory retrieval phase a question was visually presented on the screen for 5.5 seconds during which the participants could read the question and prepare their response. There was then a brief fixation cross (jittered from 0- 100 ms), and then a green X that signalled the beginning of the response phase. In the response phase, the participants were asked to answer the question aloud and the responses were recorded using a MR-compatible microphone. The subjects were given 14 seconds to respond and were encouraged to speak for the full-duration. The trials were presented using an event-related design with the most efficient ordering of events determined using Optseq (http://www.freesurfer.net/optseq). Null time was intermixed between trials and varied between 0 and 15 seconds (average = 3.82 seconds, SD = 5.95) during which a fixation cross was presented. The experiment was presented in 3 runs, each lasting 446 seconds, the order of which was counterbalanced across participants. The content of each question was matched across conditions, but the same person would never see more than one version of each item.

Autobiographical condition: Here the participants were presented with a variety of questions probing autobiographical events (e.g., describe the last time you had a cup of tea). Participants were

instructed to describe the event using as much highly specific contextual detail as possible. For example, where the event took place, who they were with, when did it happen, or any further sites/scenes/sounds associated with the event.

Semantic-event condition: These questions had a similar content to the autobiographical condition but were phrased to refer to a generalised semantic-event rather than a personal autobiographical experience (e.g. describe how you would typically make a cup of tea).

Semantic-object description: These questions were again of a similar content but instead involved an object-description rather than an event (e.g. what is tea?)

Control condition: The control condition was "Recite the months of the year". The participants continued the task for the full 14 seconds (i.e., they might complete more than one full cycle of the year). This task was used as a control for any activation associated with speech apart from that association with propositional narratives.

After the fMRI session, the participants were asked to rate each question on a 1-5 scale in terms of how vividly they could remember the event (autobiographical events only), how frequently they experienced the event (autobiographical events, and semantic-events), and how difficult they found the question to answer (all conditions).

fMRI acquisition

MRI data was collected using a Siemens 3 T PRISMA system. T1-weighted images were acquired using a 3D Magnetization Prepared RApid Gradient Echo (MPRAGE) sequence [repetition time (TR) = 2250ms; echo time (TE) = 3.02 ms; inversion time (TI) = 900 ms; 230 Hz per pixel; flip angle = 9°; field of view (FOV) 256 × 256 × 192 mm; GRAPPA acceleration factor 2]. Functional data were acquired using a multi-echo multi-band (MEMB) blood oxygenation level dependent (BOLD)-weighted echo-planar imaging (EPI) pulse sequence. The MEMB sequence had the following parameters: (TR = 1792 ms; TEs = 13, 25.85, 38.7, and 51.55 ms; flip angle = 75°; FOV = 192 mm × 192 mm, MB factor = 2, in-plane acceleration = 3, partial Fourier = 7/8). Each EPI volume consisted of 46 axial slices in descending order (3 x 3mm) covering the whole brain (FOV = 240 x 240 x 138 mm). For each session, 252 volumes were acquired.

Preprocessing

All raw DICOM data were converted to nifti format using dcm2niix. The T1 data were processed using FSL (v5.0.11) (28-30) and subjected to the 'fsl_anat' function. This tool provides a general processing pipeline for anatomical images and involves the following steps (in order): 1) reorient images to standard space ('fslreorient2std'), 2) automatically crop image ('robustfov'), 3) bias-field correction ('fast'), 4) registration to MNI space ('flirt' then 'fnirt'), 5) brain extraction (using fnirt warps) and 6) tissue-type segmentation ('fast'). All images warped to MNI space were visually inspected for accuracy. The functional MEMB data were pre-processed using a combination

of tools in FSL, AFNI (v18.3.03) (31) and a python package to perform TE-dependent analysis (32-34). Despiked (3dDespike), slice time corrected (3dTshift, to the middle slice), and realigned (3dvolreg) images were submitted to the "tedana" toolbox (max iterations = 100, max restarts = 10), which takes the time series from all the collected TEs, decomposes the resulting data into components that can be classified as BOLD or non-BOLD based on their TE-dependence, and then combines the echoes for each component, weighted by the estimated T2* in each voxel, and projects the noise components from the data (33, 35). The resulting denoised images were then averaged, and the mean image coregistered to T1 (flirt), warped to MNI space (using fnirt warps and flirt transform), and smoothed with 6 mm FHWM Gaussian kernel.

General Linear Modelling (GLM): The data were analysed using a general linear model using SPM12. At the individual subject level, each condition was modelled with a separate regressor and events were convolved with the canonical hemodynamic response function. At the individual level, each task condition was modelled separately against rest. Group analyses were conducted using standard voxel height threshold $p < .001$, cluster corrected using FWE $p < .05$. We have argued elsewhere that a comparison of a task > rest is an important an informative contrast (10, 12, 36). Given the involvement of AG in the DMN, it is of critical importance to consider whether a task positively or negatively engages the region relative to rest. Whilst many tasks generate deactivation in the AG, this is not always the case and the handful of task types that do positively engage the AG might be crucial sources of evidence about its true function (12). Contrasts between a cognitive task of interest vs. an active control condition are ambiguous because the difference could result from 1) greater positive activation for the task or 2) greater *deactivation* for the control. This issue becomes even more important when considering the impact of task difficulty on activation and deactivation in this region. A straightforward expectation applied to almost all brain regions is that if a task critically requires the AG then the AG should be strongly engaged by that task. Indeed, this is the pattern observed in the anterior temporal lobe (ATL) where semantic tasks are known to positively engage the ATL relative to rest, whereas non-semantic tasks do not modulate or deactivate ATL (36). Perhaps one of the major motivations for considering task (de)activation relative to 'rest' is that 'rest' can be used as a common constant reference point across tasks. This is particularly important when conducting cross-domain comparisons. For instance, when one is examining a single cognitive domain it is possible to use a domain-specific baseline, i.e., by contrasting a task that places strong demands on the particular cognitive system vs. a task with lower demands (e.g. remember > know in an episodic memory tasks, or words > non-words in a semantic memory task). Since the same is not possible across cognitive domains, rest acts a common constant for cross-domain comparisons, even if the true cognitive interpretation of 'rest' is unclear.

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ROI Analyses: Targeted ROI analyses were performed using an AG ROI. The AG ROI was a 8mm sphere based on coordinates from a meta-analysis on the area to show maximal likelihood of activation across semantic and episodic studies in large-scale meta-analysis (10). These results were contrasted to those from the semantic hub region (ATL) (as identified in a comparison of semantic > non-semantic contrasts across 69 participants (36)), and the autobiographical network which includes the perirhinal cortex, posterior cingulate cortex/precuneus, medial prefrontal cortex, and lateral middle temporal gyrus (as identified in a meta-analysis of autobiographical studies (23). This latter network is sometimes referred to as the posterior medial episodic system and overlaps substantially with the DMN (8, 13). If the AG is a semantic hub then one would predict a similar response to the semantic network. In contrast, if the AG is in involved episodic/autobiographical processes one would expect a similar AG response to the wider autobiographical retrieval network.

Regression Analyses: To foreshadow the results, the AG was found to be strongly engaged by the autobiographical task, but also to a minimal extent by the event-semantic task (and deactivated by the other two tasks). We predicted that the level of event-semantic activation would be modulated by variation in the memory retrieval strategy used to describe each event: the extent to which the participant draws on the semantic or autobiographical memory systems. To test this hypothesis, a parametric modulator was added to the semantic-event condition to examine the relationship between certain variables and neural activation. These variables were derived from an independent item-rating study in which items were rated on 1-5 scale by a separate group of participants. The average item-rating was added as a regressor to the analyses. There were three ratings:

1) *Event frequency*: how frequently do you experience each event? This factor might influence the reliance on a semantic vs. autobiographical memory retrieval strategy since highly frequent events would be expected to be more greatly semanticised (i.e. will have developed an "event-schema") whereas infrequent events a participant might base their answer on a more highly specific memory.

2) *Event vividness*: how vividly can you remember last experiencing each events? More vivid memories might be include more autobiographical details and may be less semantic in nature.

3) *General knowledge vs. Episodic*: to what extent would you base your response on general knowledge of how the event typically unfolds vs. a highly specific memory of experiencing the event? An event based on general knowledge would by definition recruit a semantic memory, whereas a highly-specific memory would be more episodic in nature.

4) *Response similarity analysis*: Finally, we also coded in-scanner response from the fMRI participants. Semaniticised events are long-term representations that, though repetition and rehearsal, beyond more general and independent of any one episode. Accordingly, they are reflected in generalised consistent productions across participants. Latent Semantic Analysis (LSA) was

performed on the fMRI verbal responses from the scan in order to code the level of semantic similarity across responses for each question. The average LSA score for each item was added as a regressor to the GLM analysis. It was predicted that verbal responses to items that were highly "semanticized events" would be more similar in content across individuals (hence a higher LSA score), whereas "autobiographical events" would be distinctive and include more idiosyncratic responses (a lower LSA rating).

Results

Meta-analysis

The results from the primary ALE analysis of 26 propositional speech production studies revealed a fronto-temporo-parietal network. In the fronto-temporal network, significant clusters were observed in left precentral gyrus, inferior frontal gyrus (IFG, BA44), supplementary motor area, and middle temporal gyrus. In parietal cortex, separate clusters were observed in dorsal LPC (IPS/SPL), ventral LPC (angular gyrus), and precuneus (see Figure 1).

Secondary analyses were performed in order to determine the stability of the network across domains. Specifically, we sought to determine which clusters form core parts of the propositional speech network that are unaffected by the nature of the task, and which clusters vary depending on task domain, such as whether the task involves autobiographical memory retrieval. When the six autobiographical tasks were dropped from the analysis the fronto-temporal and dorsal parietal peaks remained constant, whereas the ventral parietal cortex (AG and precuneus) were no longer reliably activated, even when the analysis was performed at a less stringent statistical threshold (uncorrected, $p < .05$) (see Figure 1). The likelihood that the modulation of ventral parietal cortex was influenced by task-domain, rather than a reduction in power, was supported by the series of random study-exclusion analyses. Here we found that that random deselection of six studies produced the same results as the primary ALE analysis including the AG/precuneus. That is, when the AG and precuneus clusters were present in the ALE results, they were solely driven by peaks from the autobiographical studies. Taken together, these analyses suggest that the AG (and precuneus) involvement is not general to propositional speech but rather to autobiographical retrieval (see Table 1). Together these data suggest that AG does not form part of the core propositional speech network, rather it is only reliably activated when a task places requirements on the autobiographical memory system.

fMRI results

Autobiographical retrieval vs. semantic retrieval: During the memory retrieval phase, all experimental conditions were found to activate a widespread fronto-temporo-occipital network. In

addition, the autobiographical condition was found to strongly activate the AG, as well as other areas that are known to form the default mode network (medial fronto-parietal structures and hippocampus). The semantic-event condition did weakly activate the AG, however, the cluster was comparably smaller and limited to the anterior portion of AG, and there was little involvement of the wider DMN (Figure 2). The semantic-object condition showed no AG (or DMN) activation. Direct contrasts between conditions showed significantly stronger AG and DMN activation for the autobiographical condition compared to either semantic task (Figure 2). During the response phase, all tasks showed activation in areas associated with motor output (frontal lobe, insular, basal ganglia) as well as language areas in the temporal lobe. As per the results from the memory retrieval period, the AG was activated for the autobiographical task (and no other task), although the level of activation was lower and the cluster reduced in size compared to the memory retrieval phase (see Figure 2 showing whole brain results for each phase, and Figure 3 showing the ROI results for AG, ATL, and autobiographical memory ROI to compare the signal magnitude of each phase). Indeed, an examination of the activation time-course showed that whilst the AG was activated throughout the question and response phase of the trial, it was more strongly associated with the memory retrieval phase, rather than response phase of the trial thereby suggesting a primary role in autobiographical memory retrieval. Accordingly, the remainder of the analyses focussed on the memory retrieval phase of the experiment (further analyses from the response phase can be seen in Supplementary 1.

ROI analyses of the AG showed a strong positive activation for the autobiographical condition relative to rest ($t(27) = 9.54$, $p < .001$), and significantly greater activation relative to all other conditions (all ts > 8.00, all ps < .001). AG also showed significant positive activation relative to rest for the semantic-events ($t(27) = 4.13$, $p < .001$), as well as greater activation for the semantic –events relative to semantic-objects (which did not differ significantly from rest ($t(27) = 2.18$, $p = .06$)), and control (which deactivated the AG ($t(27) = -2.35$, $p = .02$)) (all ts > 3.77, all ps < .001) (Figure 3). The exact same pattern was also found in the wider autobiographical memory network (all ts > 4.48, all ps < .001) (Figure3). Together these results show that the AG is primarily involved in autobiographical memory and shows a similar response to the wider autobiographical network. In contrast, the ATL showed equally strong involvement for all experimental conditions (all ts < 1.76, all ps > .09), which was significantly greater than rest (all ts > 8.22, all ps < .001), and control (all ts > 10.26, all ps < .001) (Figure 3). This is consistent with the role of the ATL as a semantic-hub, and is thereby activated by any task requiring semantic retrieval. For comparable analyses from the response phase, see Supplementary 1: Briefly, in the AG, the autobiographical task showed greater activation relative to all other tasks, which otherwise deactivated AG. In contrast, the ATL showed equal activation for all experimental conditions, which was greater in magnitude relative to control.

Semantic-events vs. semantic objects: Directly contrasting the event-semantic and object-semantic tasks showed significantly stronger recruitment for semantic-event descriptions within the posterior middle temporal gyrus (pMTG), an area associated with multiple functions (motion-

processing, verb processing, semantic control), and superior parietal lobe (SPL), whereas object-semantics showed increased activation of visual cortex, which could reflect the use of visual imagery during object description.

Regression analyses

The GLM results demonstrate that the AG, like other regions of the autobiographical network, was strongly activated by the autobiographical memory task. There was also some evidence of AG activation for the event-semantic task, albeit at a lower magnitude. This is a very different pattern to that observed in the semantic memory network (including the ATL) where equal activation was found for all tasks. Whilst the AG was clearly activated during autobiographical memory retrieval, what was driving the limited activation for the event-semantic task? The results of four regression analyses indicated that the AG response to the event-semantic task was driven by the extent to which the participants were relying on an autobiographical retrieval strategy to respond to each question, rather than a semantic retrieval strategy. Specifically, we hypothesized that a low frequency highly vivid event is less likely to be semanticised and more likely to rely on autobiographical memory retrieval. Consistent with this hypothesis, ROI analyses showed that AG activation was: 1) negatively related with event frequency ($t(27) = -3.89$, $p = .001$), and 2) positively with event vividness ($t(27) = 3.81$, $p = .004$). Furthermore, 3) there was a positive relationship with participants' subjective rating of the extent they based their response on a specific memory rather than general knowledge ($t(27) = 5.23$, $p < .001$). Finally, 4) a negative relationship was found between AG activation with the response similarity ratings, as computed by the LSA semantic similarity analysis ($t(27) = -6.75$, $p = .001$). This pattern can be clearly seen when conducting a median split analysis based on high vs. low ratings on each measure: as the item becomes more autobiographical in nature the activation increases, closer to that of the autobiographical task (Figure 4). Together these results suggest that the AG is engaged when an event is based on autobiographical rather than semantic memory. Compellingly, a similar profile was found across the wider autobiographical network (all $ts > 2.34$, $ps < .008$). This result is in sharp contrast to that found in semantic areas, such as the ATL, which were invariant to each of these variables, showing equal response regardless of the ratings (all $ts < .9$, $ps > .4$). The fact that the AG results mirror that of the episodic rather than semantic network provides strong evidence in favour of an episodic/autobiographical rather semantic function of the AG in memory retrieval.

Discussion

The current study focused on comparing the AG engagement with three types of memory using the previously under-examined naturalistic task of propositional speech production. The results from the meta-analysis indicated that the AG is only engaged as part of the propositional speech

network when the task carries an autobiographical component. This conclusion was strongly supported by the results from the fMRI study. The key fMRI findings were: 1) AG is positively engaged during autobiographical memory retrieval and activation increases with the degree to which a task relies on input from the episodic memory system. Indeed, elsewhere we have shown that the same AG ROI shows strong functional and structural connectivity with the episodic network (9, 12). 2) The AG showed a very different response to the ATL semantic hub – whilst AG activation increased with the autobiographical nature of the task, the ATL was equally responsive to all conditions, in contrast a similar response was found in the AG to the wider autobiographical network. This provides clear evidence that the AG is not acting as a semantic hub. 3) Activation was strongest during the memory retrieval phase rather than the response phase of the trial.

Implication for episodic research

The current data are consistent with a wealth of studies showing positive AG activation during autobiographic/episodic retrieval tasks, with activation correlated with memory vividness (12, 37-39). We propose that information stored elsewhere in the episodic system is temporally buffered online in the AG during episodic retrieval/memory construction. Indeed, the notion of an AG episodic buffer has been proposed elsewhere (1, 2), and fMRI evidence has shown that, unlike the hippocampus that responds to boundaries between episodic events, AG activation is maintained throughout an event, consistent with the role of the AG as an online buffer of retrieved information (40-42). The buffer model is also consistent with neuropsychological evidence showing that, unlike medial temporal damage, parietal damage does not result in profound amnesia but rather it results in a lack of clarity or vividness of autobiographical details, which one might expect from a deficit in the buffering of multi-modal contextual information (11, 43-50).

Implication for PUCC

The current data are consistent with the PUCC model, which proposes that the LPC acts as online buffer of information, in this case relating to autobiographical episodes. According to PUCC, variations in activation across LPC arise from variations in long-range connectivity (9-12). This tenet has been formally demonstrated by computational models, whereby the resultant "expressed behaviour" of a group of processing units depends not only on their local computation, but also on the long-range connectivity (more recently referred to as 'connectivity-constrained cognition – C^3': (51-53)). Indeed, we have proposed two primary axes of LPC organisation: dorsal-ventral and anterior-posterior. Driven by top-down input from the prefrontal cortex (54), the dorsal LPC is actively engaged by executively demanding tasks across cognitive domains (10, 55, 56) and may be involved in the selection and/or manipulation of buffered information, akin to an executively-penetrated working memory system (10, 57). In contrast, we have shown that in the ventral LPC there is an anterior-posterior gradient of activation, with more anterior regions positively engaging

during sentence/narrative comprehension and show structural/functional connectivity with the language network, mid-AG is positively engaged during episodic/autobiographical and this is driven by strong functional and structural connectivity with the episodic memory system, and more posterior LPC showing positive engagement for picture-sequences, and connecting with visual cortex (9, 12). When a task does not involve the cognitive process of interest, that particular ventral LPC subregion is deactivated – hence the common observation of AG task-related deactivation.

A system concerned with temporal buffering would be particularly useful for tasks that are reliant on information that unfolds over time. Indeed, parietal damage can produce deficits in performing time-extended verbal and non-verbal behaviours (e.g., logopenic progressive aphasia, ideational apraxia, etc.) (58, 59). Furthermore, the anterior AG is engaged by sentence processing and narrative speech comprehension (9, 10, 60, 61) and the AG shows a reliable response to narratives and movies when the content is intact rather than temporally scrambled (62, 63). The indication that the AG is more strongly activated during the memory-retrieval phase than the response phase of the trial has implications for the nature of the PUCC buffering system. Specifically, these findings are more consistent with the AG acting as an “input” rather than “output" buffer whereby LPC buffers temporally-extended external and internal inputs, rather than controlling or monitoring the roll out of temporally-extended behaviours. Indeed, the finding that the system was not activated during speech output is consistent with evidence that the area is not reliably activated by other types of speech output tasks, e.g., verbal fluency (64). Furthermore, outside of speech production, the AG has been found to be more active when imagining the words to a familiar song than listening to the same song, supporting the notion that the region is sensitive to the processes involved in memory retrieval, rather than the external stimulus itself (65).

In terms of a mechanistic account of how the buffer might operate, two possible alternatives can be contemplated. First, temporally-extended behaviours are often thought to rely upon a stored “task-schema” (66-68). Accordingly, the buffer might keep track of not only the evolving state of play but also the remaining steps needed to transform a particular “thought” into speech output (the future steps). Given that the AG appears to be differentially activated for the retrieval vs. speech phase of autobiographical production, then this schema-based hypothesis seems less likely. Alternatively and consistent with the current data, the AG might only buffer incoming spatio-temporally varying information, and does not contain information with regard the future steps required to transform the “thought” into action (69, 70). This approach allows for greater flexibility in real-world unpredictable situations, since an ever-changing context will lead to variability in the outcome of a sequence each time it is performed.

Implications for semantic research

The current data provide clear evidence that the AG is not engaged during semantic retrieval, supporting findings elsewhere (10, 12, 56). This is consistent with evidence showing that parietal damage does not result in gross semantic-memory retrieval impairment (unlike damage to the ATL), but rather in the flexible use and manipulation of semantic information (71). The current data also go one-step further by demonstrating that the AG is not sensitive to all semantic-events, rather activation is driven by the extent by which event-retrieval relies on input from the autobiographical/episodic memory system.

How can one align the lack of semantic modulation, found here and elsewhere, with neuroimaging results showing an apparent sensitivity to semantic contrasts or semantic-events in the AG (5, 6)? As mentioned in the Introduction, when studying LPC function it is important to take into account certain critical variables: 1) the polarity of activation relative to rest and 2) difficulty-related differences. With regard the polarity of activation, direct comparisons have shown that, whereas the ventral LPC is positively engaged during episodic retrieval, the same region is deactivated relative to rest during semantic retrieval tasks (10, 12, 56). It is of course difficult to interpret "rest", as it may involve spontaneous semantic and linguistic processing (72) (although the same argument would presumably also apply to episodic retrieval which shows positive task-related activation (7, 8). Critically, however, the AG semantic-hub hypothesis is inconsistent with the observation that the AG shows a very different pattern to other semantic-hubs, such as the ATL, which is *positively* engaged during semantic retrieval (36, 56), and shows constant activation across conditions in the current study (presumably due to the fact that all conditions contain meaningful elements and entities, and speech production is driven by semantics). With regard to task-difficulty, the contrast of word > nonword and concrete > abstract typically involve comparing an easier task vs. a harder task, and AG deactivation is known to relate to task difficulty, with increasing deactivation for harder tasks (56, 73-75). Indeed, direct examinations of task difficulty in semantic and non-semantic tasks have revealed a main effect of task difficulty (easy vs. hard) on the degree of deactivation in the ventral AG but no semantic vs. non-semantic difference (76, 77), and compellingly, the classic pattern of differential activation associated with the contrast of words > non-words or concrete > abstract processing, can be flipped by reversing the difficulty of the task or the stimuli (78, 79). A similar argument might also explain results from studies of combinatorial-semantics, where 'higher' AG 'activation' is associated with adjective-noun or adjective-verb word pairs that are readily-combined compared to less automatic combinations (80, 81).

Implications for models of speech production

The current meta-analysis constitutes the largest meta-analysis of the propositional speech production literature. Together with the results from the fMRI study, the data have implication for models of speech production. Specifically, the results show that the core speech production network

is made up of frontal areas (IFG, precentral gyrus, and SMA), and temporal areas (middle temporal gyrus, and the ATL). In contrast, the AG plays a task-specific role. Several researchers have proposed a dual-stream model of language, where the neural mechanisms that underlie language can be separated into dorsal and ventral processing streams (82-84). Perhaps the best-known of the dual-stream models proposes that language production and comprehension rely on separable dorsal and ventral processing streams, respectively (84). Here, the ventral route consists of posterior and ventral temporal cortex for receptive speech, whereas the dorsal stream consists of dorsal posterior temporal cortex and posterior frontal areas, with the frontal cortex serving a primarily a motoric role in speech output. The current data show that both dorsal and ventral fronto-temporal networks are implicated in the core speech production system. More specifically, we found extensive frontal activation during speech production, however we argue for a broader role of frontal cortex in speech production beyond the obvious motor component of the task, such as executive control and working memory processes. Indeed, frontal activation extended into ventral IFG, known to be involved in semantic control of speech comprehension and production as well as nonverbal tasks (85-88), and areas overlapping with the multi-demand network (DLPFC and SMA) involved in domain-general executive processing (55). In terms of the contribution of the temporal lobe, the full length of the MTG and ventral ATL were strongly activated across conditions in the fMRI study. The posterior MTG has been associated with semantic control (85, 86). In contrast, the more anterior MTG is known to be active during sentence-level tasks during speech production and comprehension (60, 89-91), and may play a role in combinatorial processes (92). In terms of the ventral ATL, there is strong evidence that the ATL is multi-modal semantic hub (86). For instance, the contribution of the ATL to speech production and comprehension is well-established in the neuropsychological literature whereby semantic dementia patients show significant deficits in both expressive and receptive semantic tasks (71) including impoverished content in propositional speech tasks (93, 94) Furthermore, ATL engagement during semantic tasks has been consistently shown using fMRI and TMS in healthy participants and intracortical grid electrode studies in neurosurgical patients (10, 95-98). Reliable ATL activation was less obvious in the meta-analysis (although still present at a reduced threshold). This absence of evidence in the meta-analysis is very likely to be due to various methodological issues including fMRI signal loss in most single echo EPI fMRI paradigms (95, 99). The current fMRI study utilised a multi-echo paradigm designed to improve signal coverage thereby revealing strong ATL modulation across semantic conditions (100)

Conclusions

To conclude, we demonstrated here that AG activation depends on the extent to which a task requires input from the autobiographical-, rather than semantic-memory retrieval systems. The results are consistent with a model in which the LPC acts as a multi-modal buffer and subregional

variations in expressed functions reflect differences in their long-range connectivity; the AG gravitates to episodic-related tasks as a result of its preferential connectivity to the episodic network.

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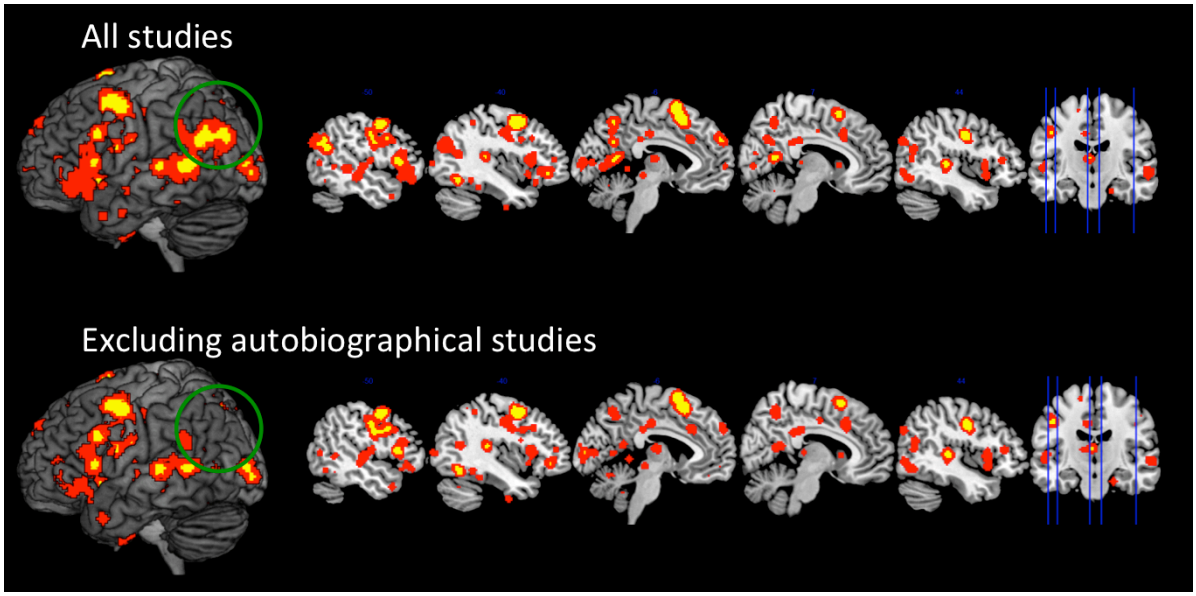

Figure 1. Top panel. The results from the ALE meta-analysis when including all 26 propositional production studies. Bottom panel. The results from the ALE meta-analysis after excluding autobiographical studies. Yellow indicates clusters significant at $p < 0.001$ (with cluster-level FWE-correction of $p < 0.05$), and red indicates clusters corrected at the lenient $p < .05$ threshold.

		All studies	Excluding Autobiographical studies	V1	V2	V3	V4	V5	V6	V7	V8	V9	V10
N studies	Cluster	26	20	20	20	20	20	20	20	20	20	20	20
Parietal	IPS/SPL	+	+	+	+	+	+	+	+	+	+	+	+
	AG cluster 1	+	-	+	-	-	+	+	+	+	+	+	+
	AG cluster 2	+	-	+	+	+	+	+	+	+	+	+	+
	Precuneus cluster 1	+	-	+	-	-	+	+	+	-	+	-	+
	Precuneus cluster 2	+	-	+	-	-	+	+	+	-	+	-	-
Temporal	MTG	+	+	+	+	+	+	+	+	+	+	+	+
Frontal	SMA	+	+	+	+	+	+	+	+	+	+	+	+
	Precentral gyrus	+	+	+	+	+	+	+	+	+	+	+	+
	IFG BA44	+	+	+	+	+	+	+	+	+	+	+	+

Table 1. The neural areas that showed significant clusters from the ALE analysis when including 1) all 26 studies, 2) Excluding autobiographical studies, 3) The random study-exclusion analyses, version1 (V1) to version 10 (V10).

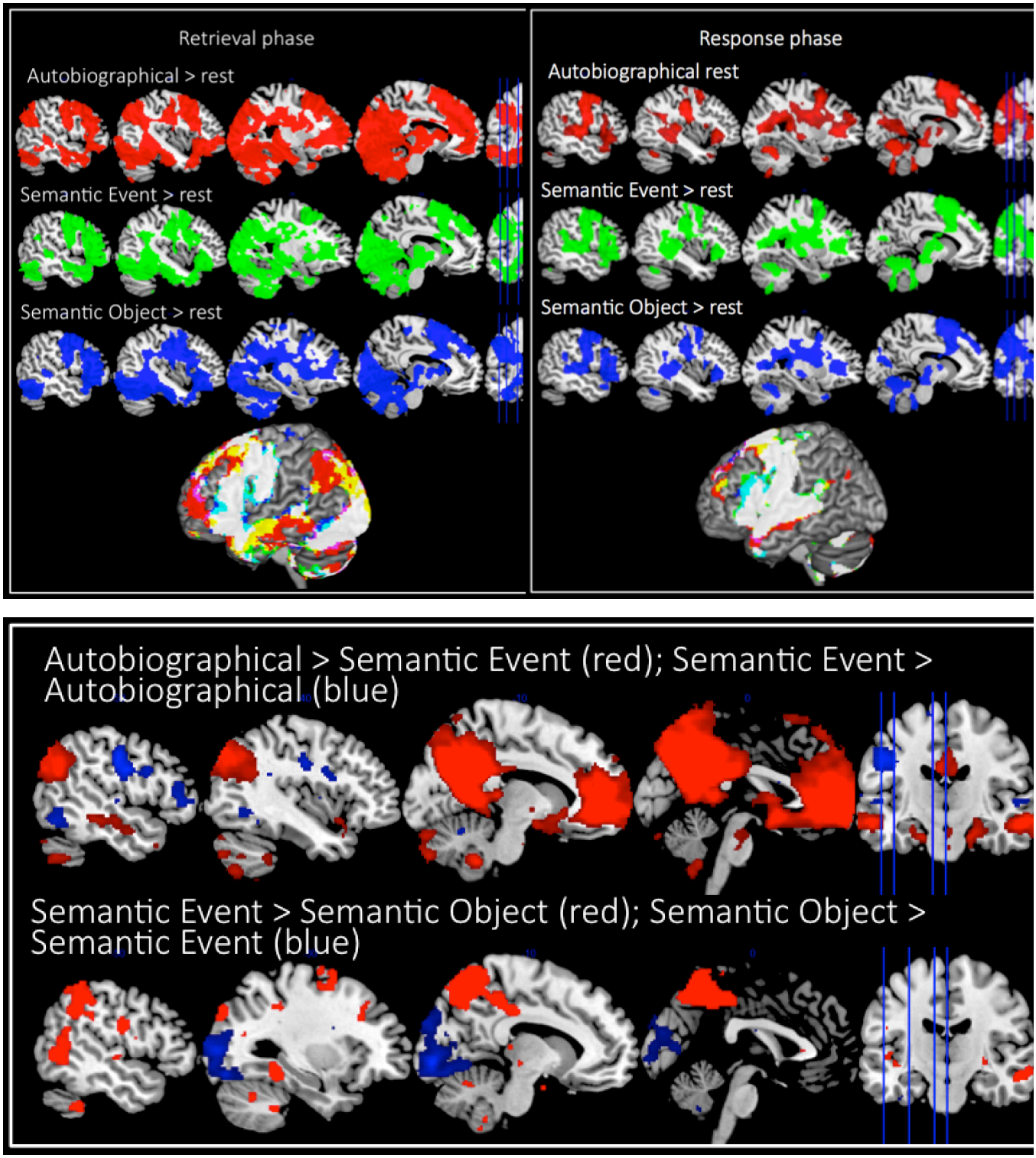

Figure 2. The fMRI results from each task > rest from the "retrieval phase" (top left), "response phase" (top right) (yellow, white, cyan, violet reflect overlapping activations), and the direct task contrasts (bottom). Voxel height threshold $p < .001$, cluster corrected using FWE $p < .05$

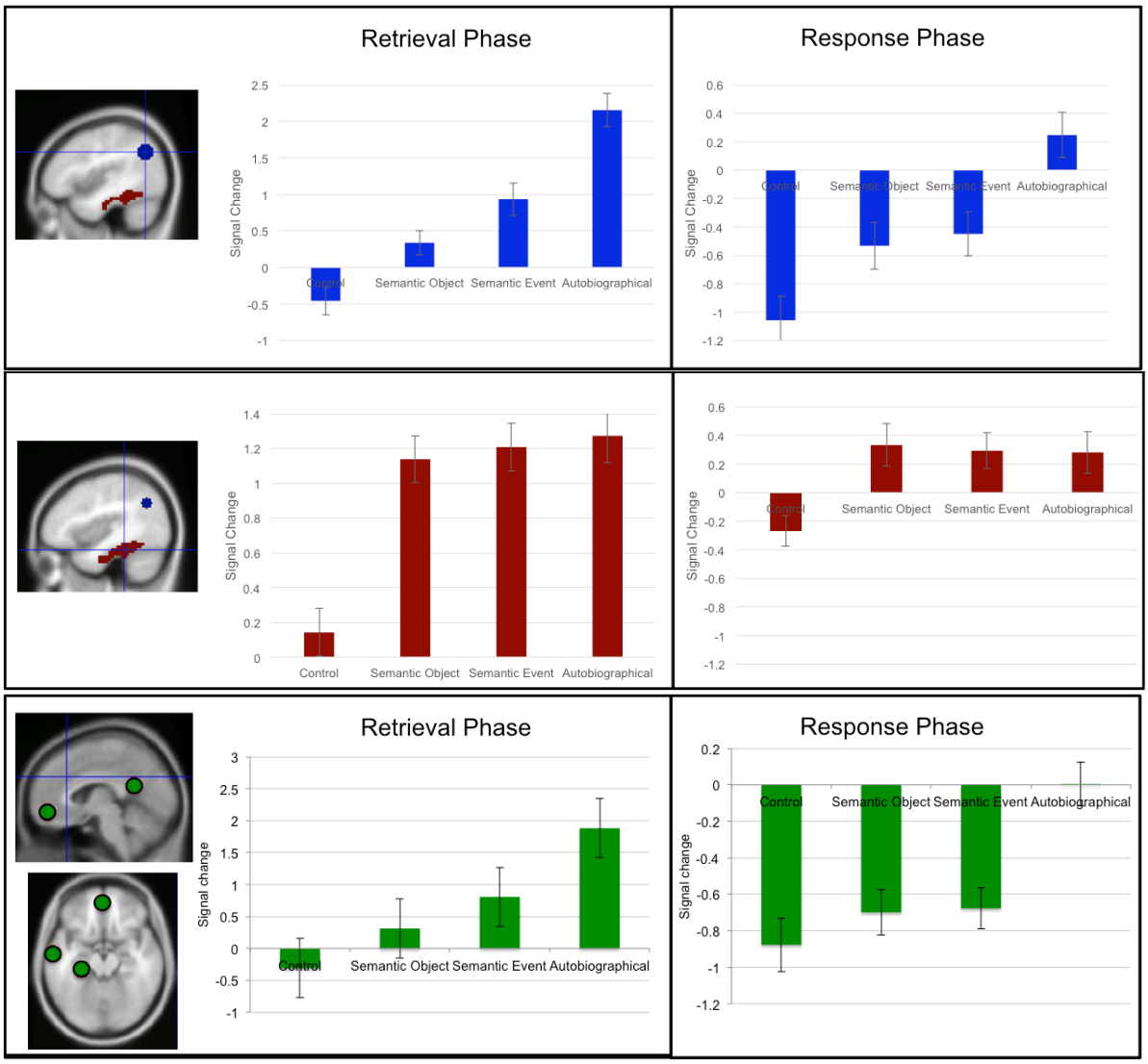

Figure 3. ROI results showing the signal change for each condition relative to rest in AG (blue), ATL (red), and autobiographical network (green).

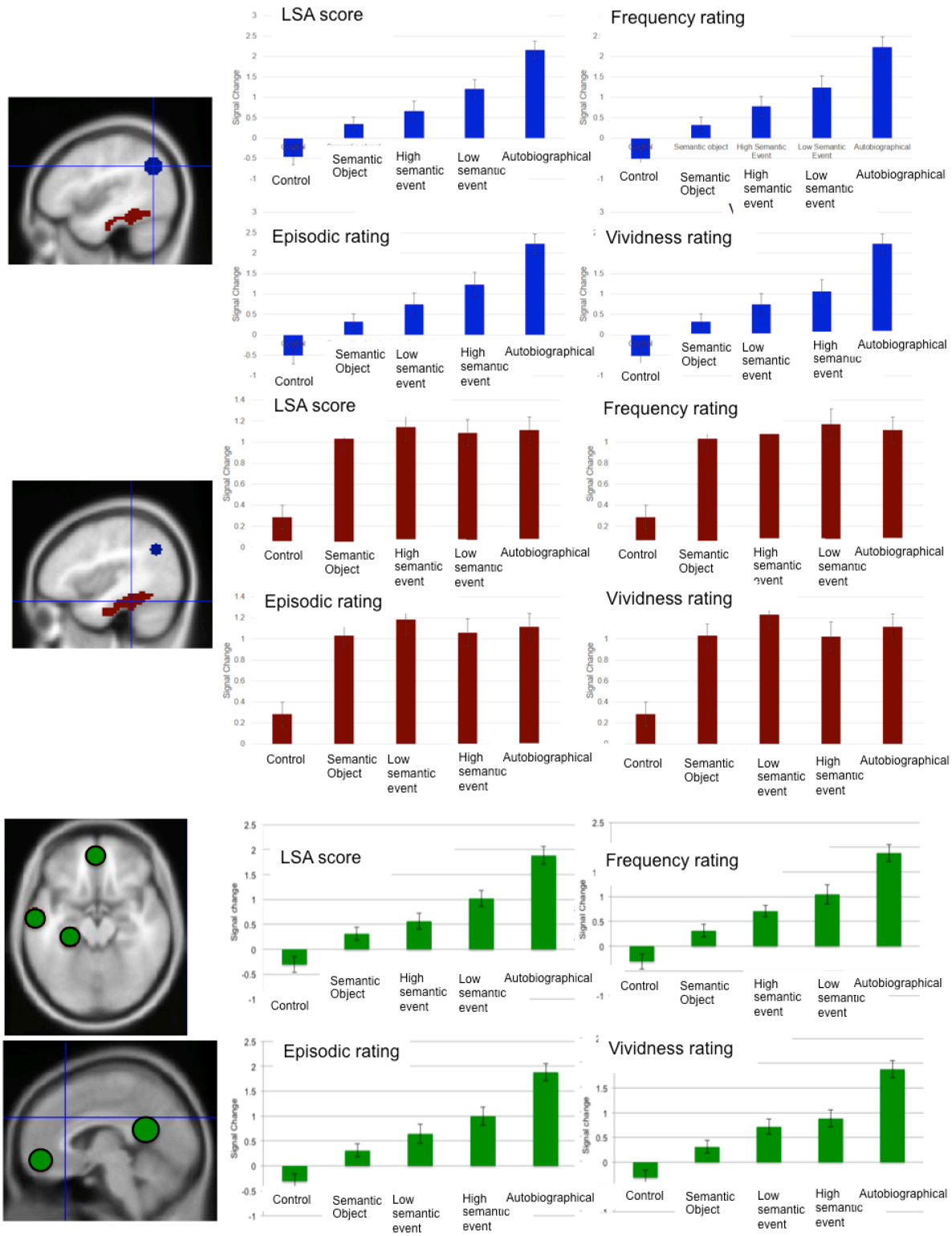

Figure 4. ROI results showing the signal change for each condition relative to rest in AG (blue), ATL (red), and autobiographical network (green). The Semantic-Event condition is split into a high vs. low condition based on a median-split using the ratings from the response similarity (LSA), Frequency, Episodic relatedness, and Vividness analyses.

Supplementary Information

ROI analyses from the response phase of the experiment: the AG showed significantly greater activation for the autobiographical condition relative to all other conditions (all ts > 6.29, all ps < .001). The AG did not differ in response to the semantic-events and semantic-objects ($t(27) = 1.19$, $p = .25$), although both conditions differed to control ($t(27) = 3.40$, $p < .005$). With the exception of the autobiographical condition, all conditions showed significant deactivation relative to rest (all ts > -2.90, all ps < .005). The same pattern was found for the wider autobiographical network. Unlike the AG, the ATL showed no significant difference between conditions (all ts < 1.27, all ps > .22) and all tasks were greater than control (all ts > 6.22, all ps < .001).